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Revision of the Milliped Genus *Cleptoria* (Polydesmida: Xystodesmidae)

By Richard L. Hoffman [1]

The present paper is concerned with a small group of xystodesmids occurring in Georgia, South Carolina, and Alabama. There is no doubt that these forms are closely related and comprise a homogeneous entity. There is, however, a very real problem concerning the formulation of an opinion about their relative taxonomic status. As will be subsequently pointed out, it is becoming increasingly difficult to draw suitable definitions for several nominal genera set up for American xystodesmids in recent years, genera that were initially distinct only because they happened to be monotypic or contained only a few species.

In the present instance, some students of Diplopoda will surely contend that the species here treated as the genus *Cleptoria* cannot be set off precisely from other groups of southeastern xystodesmids and should at most be given the status of a "species-group." While I admit that this contention is probably a valid one, it seems in the present state of our knowledge that the designation of such groups by a generic name makes it slightly easier to categorize them for convenience in classification. Later, when the fauna has been thoroughly developed and all of the species accounted for, it will

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be appropriate to re-evaluate these groups and adjust their status in the hierarchy accordingly. In the meantime, we must go ahead with the procedure that is more expedient in accomplishing the initial goals.

The preliminary work upon which the following synopsis is based was done more than a decade ago and forms the basis for the arrangement of the genus in the "Checklist of the Millipeds of North America," in which three valid species were recognized. Present departure from this arrangement lies in the addition of two new species and a new subspecies, the transfer into *Cleptoria* of a form originally described in *Sigmoria*, and the transfer out of *Cleptoria* of one species into a new genus as yet unpublished. Surprisingly few specimens have been available for study despite the extensive field work done by Leslie Hubricht in the southeastern States.

The first species referable to the genus *Cleptoria* as currently conceived was described by C. H. Bollman in 1889, under the name *Fontaria rileyi*, on the basis of a single male taken at Macon, Ga., by L. M. Underwood. The male gonopods were not illustrated, but the descriptive phrase "terminal end subsimilar to a bird's head" made it possible for Dr. R. V. Chamberlin to associate *F. rileyi*, in the original proposal of *Cleptoria* (1939), with his type-species *C. macra*. In 1943, *C. macra* was synonymized under *C. rileyi* by H. F. Loomis, who had seen Bollman's type-specimen and had felt that the two nominal species were identical; in the following year (1944) Loomis described *C. shelfordi*. Since then, no further published references pertaining to the genus have appeared other than the "Checklist" (1958), in which *C. macra* is reinstated as a valid species without comment. In the same paper, however, in which *Cleptoria* was proposed, Chamberlin also described a species under the name *Sigmoria divergens;* more recently, I (1950) added an additional form, *S. nigrescens*, that has an obvious affinity to *S. divergens*. A restudy of both of these forms indicates that the relationship between them is subspecific at best and that *S. divergens* should be transferrred to *Cleptoria*.

I have been fortunate in being able to restudy the type-specimens of all of the species mentioned above. Dr. R. V. Chamberlin (RVC) very kindly lent the types of *C. macra* from his personal collection in 1948 and facilitated their re-examination in 1963. Dr. P. J. Darlington kindly allowed access to the type of *C. shelfordi* at the Museum of Comparative Zoology during a visit of mine in 1949. The collection of the U.S. National Museum, under the care of Dr. Ralph E. Crabill, contains not only the type of *Fontaria rileyi*, but specimens of a related form from Alabama that had been recognized as new and so labeled by O. F. Cook over 60 years ago.

I have been able to secure only one member of the genus through personal collection, and all of the new material at hand springs from the unflagging diligence of Leslie Hubricht, who has generously sent me material of all of the species here considered valid, including the two undescribed forms. It would not be incorrect to state that our expanding knowledge of American diplopods is due in large measure to Mr. Hubricht's skill as a collector and his willingness to devote time and effort to the collection of specimens outside of his own special area of interest.

My own field experience with *Cleptoria divergens* has been implemented by grants administered by the Highlands Biological Station. The synthesis was commenced at the U.S. National Museum in 1959 and completed at Radford College in 1963 with the support of grants (G–9805 and G–21519) from the National Science Foundation.

Taxonomic Characters

GONOPODS.—As usual, the gonopods offer specific characters of primary importance in the recognition of species. Attention may be called to one feature that is somewhat more variable and significant than in other related xystodesmid genera: the course of the seminal groove on the distal half of the telopodite.

Basically, the telopodite in *Cleptoria* is rather short and massive, and usually bent nearly at a right angle or strongly curved (in *C. divergens*), as shown in figures 7, 9, 14, and 18. The prefemoral area is small and either mutic or with only a small spur on the lateral side. The abruptly narrowed and compressed femoral region, where the angulation occurs, usually has a rather distinct flange-like lateral edge, most distinctive in *C. macra* (fig. 6), where it comes to a prominent angular termination. The distal third of the telopodite has a characteristic appearance ("shaped like a bird's head . . . ." in the opinion of Bollman) in that the apex is strongly recurved proximad, usually with a prominent rounded enlargement on the outer surface. This distal change in direction is strongly reflected by the course of the seminal groove, which runs out on the inner side of the femoral flange and then turns proximad at about a right angle. In several species, such as *C. rileyi*, *C. abbotti*, and *C. divergens*, the extreme end of the distal area is convex and striate on the lateral side, forming a kind of short, heavy solenomerite. This area is flat and smooth in *C. bipraesidens* and *C. macra*. In *C. macra* also, the seminal groove runs along the outer edge of the basal postfemoral region instead of its approximately medial location in the other species.

In *C. abbotti* the prefemoral region is unusually enlarged and the postfemoral elements considerably reduced in size; the telopodite in this species accordingly is about the most massive in form that I

have seen in the family. The subterminal outer postfemoral lobe not only is enlarged but also is reflexed somewhat proximad toward the seminal groove and is overhung partially in that area.

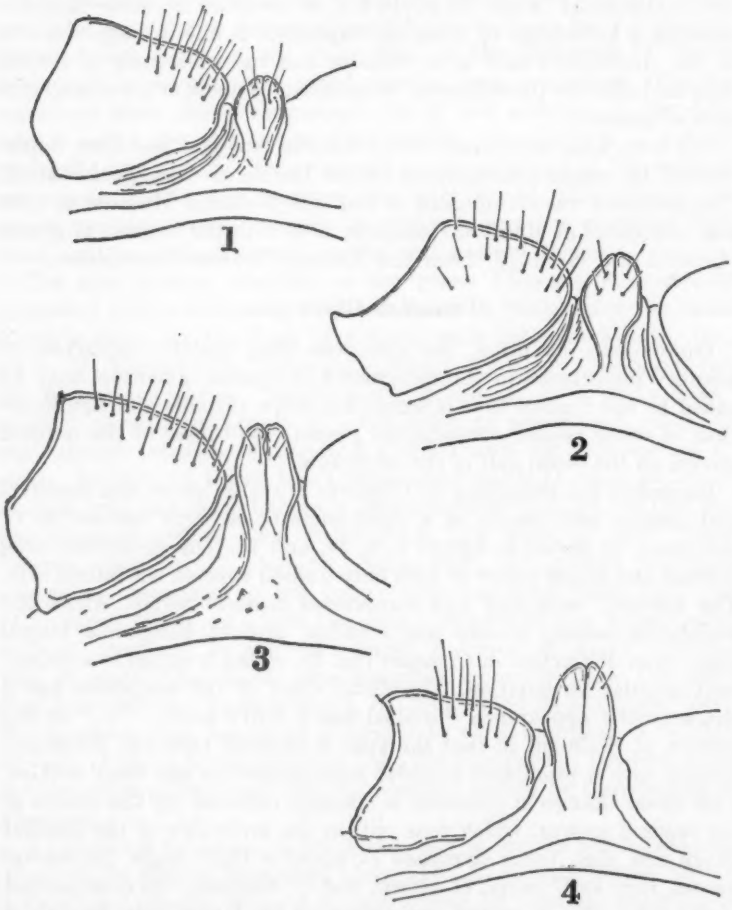


FIGURE 1–4.—Median sternal process of third segment, caudal aspect, in four species of *Cleptoria:* 1, *C. divergens;* 2, *C. rileyi;* 3, *C. macra;* 4, *C. abbotti.*

STERNA.—The sternum of the third segment in the male is modified by being produced distally into two elongate midventral lobes that are coalesced except for the extreme apices. As shown in figures 1–4, these sternal knobs extend ventrad almost as far as the ventral

surface of the coxae; they are longest in *C. macra* and shortest in *C. divergens*, in the latter of which they are of a size about normal for the family. These lobes are actually not sufficiently different in appearance to be useful in species diagnosis, but they do afford a secondary measure of specialization in the genus. Apparently their size is correlated with divergence in gonopod characters.

COLORATION.—The distribution of metatergal pigmentation is not yet well known enough to be discussed in any detail. The characteristic coloration for most of the species is that of a very dark brown dorsum with deep reddish paranotal spots and red legs. The holotype of *C. macra*, however, was recorded as having yellow spots. Whether this is a normal phenotypic variation is uncertain. In *C. bipraesidens* the paranotal red spots are linked by broad red crossbands on each metatergite. *C. divergens* and its nominal subspecies show an unusual pigmentation of intense bluish-purple or violet paranotal spots and crossbands, a coloration so far known only in two other species of xystodesmids.

Genus *Cleptoria* Chamberlin

Cleptoria Chamberlin, 1939, p. 9.—Chamberlin and Hoffman, 1958, p. 28.

TYPE-SPECIES.—*Cleptoria macra* Chamberlin, 1939, by original designation.

DIAGNOSIS.—A genus of large robust xystodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; relatively large and compact in form, W/L ratio varying from 23 to 26 percent. Head of normal appearance, smooth, polished, genae not or but moderately impressed, interantennal isthmus rather broad (up to one-fourth antennal length); facial setae reduced, epicranial, interantennal, and frontal setae absent. Epicranial suture distinct, not ventrally bifid. Antennae extending caudad to posterior edge of third metatergite; distally with four sensory cones, no other sensory structures.

Terga of body segments generally smooth middorsally, becoming coriaceous laterally toward and on paranota; latter broad, depressed, continuing slope of dorsum, peritremata broad, flattened, and elevated above adjoining discal surface; ozopores large and distinct, in normal sequence, opening dorsolaterally. Prozonites and metazonites of about same diameter, separated by fine, slightly elevated suture line at front side of stricture, latter shallow middorsally, becoming most sharply defined laterally at level of stigmata.

Posterior segments of typical appearance for family; hypoproct broadly rounded to transversely oval, with (usually) or without distinct median projection.

Sterna gradually but distinctly elevated, beginning flush with caudal edge of stricture, to form thin, overhanging transverse shelf between coxae of posterior pair of legs of each segment, this shelf usually flattened or depressed medially and produced into prominent subcoxal lobes ("bilobed sterna" of my 1965 classification). Each metasternum usually with a field of 6 to 10 setae adjacent to base of each posterior coxa and short transverse row of setae at base of each anterior coxa.

Legs moderately long and slender; coxae distally produced into small acute spines; prefemora with longer, slightly curved distal spines. Pretarsi (tarsal claws) slender, bisinuately curved, distinctly compressed, and with prominent carinae on dorsal side. Sides of segments nearly smooth, caudal edge of metazonite set off by fine elevated marginal ridge preceded by depression in most species. Stigmata large, pyriform-oval, subauriculate.

Anterior legs shorter and heavier in males but not otherwise modified. Sternum of third segment produced into prominent, bilobed process between third pair of legs; sternum of segment 5 with two pairs of small lobes or elevated areas between legs.

Gonopods unusually large and robust, projecting forward between legs of sixth segment, telopodites overlapping or interlocked. Coxae massive, subglobose, without dorsal apophysis, connected by membrane only, no sternal remnant evident. Prefemora small, with or without small subtriangular process on dorsal side, femora abruptly more slender, setose on lateral side, postfemoral element without evident differentiation, usually prominently enlarged and flattened, often with broad flange on medial side, apex recurved or bent proximad at angle, usually a smaller and more sharply defined apical projection carrying the seminal groove to the end.

Cyphopods massive, subquadrate in general outline (figs. 15, 16), receptacle forming at least a right angle and thus enclosing valves on at least two sides; valves large, distally excavate, and transversely striate; operculum small and displaced strongly proximad.

RANGE.—Piedmont physiographic province of southeastern United States, from west-central South Carolina, south into Georgia, west as far as extreme eastern Alabama (fig. 12).

SPECIES.—Five species, two of them having two subspecies each, are recognized as valid. One species, *C. shelfordi* Loomis (1944, p. 172), is removed herewith from *Cleptoria* pending relocation in another generic group so far unpublished. The members of *Cleptoria* appear to be localized, and several additional species are to be anticipated with further field work in Georgia.

Key to Species of *Cleptoria*

1. Telopodite of gonopod elongate, sigmoidally curved, the gonopods in situ usually interlocked distally; dorsum black with purple or violet paranota and crossbands . . . . . **divergens** Chamberlin, p. 21

Telopodite of gonopod short, massive, at most somewhat twisted, the gonopods in situ occasionally overlapping each other but never distinctly interlocked; dorsum blackish with markings of red or yellow 2

2. Gonopod with an acute, distinct prefemoral process 3

Gonopod without trace of prefemoral process 4

3. Prefemur exceptionally robust and massive in form; seminal groove running along middle of telopodite distally, terminating on a prominent convex retrorse solenomerite (fig. 14), subterminal lobe of telopodite prominent, rounded, abruptly reflexed toward the flexure of the seminal groove.

abbotti, new species, p. 18

Prefemur of normal dimension; seminal groove running along the outer edge of the telopodite arc for a short distance, terminating on a small, flat, scarcely distinguishable solenomerite (fig. 6); subterminal lobe of telopodite distinct but not reflexed. . . . . **macra** Chamberlin, p. 7

4. Solenomerite short, broad, distinctly convex, the seminal groove paralleled by numerous fine but distinct striations . . . . . **rileyi** Bollman, p. 11

Solenomerite elongate, relatively slender, flat and laminate.

bipraesidens, new species, p. 17

Cleptoria macra Chamberlin

FIGURES 3, 5, 6, 12

Cleptoria macra Chamberlin, 1939, p. 9, figs. 36, 37.—Chamberlin and Hoffman, 1958, p. 28.

Cleptoria rileyi Loomis, 1943, p. 393.

TYPE-SPECIMENS.—Male holotype and female paratype, RVC, from Taylors, Greenville County, S.C., collected by R. V. Chamberlin, Aug. 5, 1910.

DIAGNOSIS.—A relatively small member of the genus, paranotal spots reddish-pink (yellow), gonopod slender without prominent flange on medial face, seminal groove forming two right-angle turns, solenomerite small, short, not convexly elevated.

DESCRIPTION OF HOLOTYPE.—Body large, robust; length 50 mm, greatest width 12.0 mm; W/L ratio 24 percent; sides of body subparallel, segments 5–15 of approximately full width. Dorsum arched, paranota broad and interrupting slope of middorsum.

Head smooth and polished, slightly convex, facial surface nearly flat, epicranial suture distinct; genae convex, not margined, with only very faint median impressions; labral setae about 18, clypeal setae about 22, series extended onto lower end of genal margin. Vertigial, interantennal, and frontal setae not detected and presumably absent. Interantennal isthmus rather broad (25 percent of antennal length).

Antennae fairly long (7.5 mm) and slender, extending caudad to posterior edge of third segment. Article 1 subglobose with a few long setae on dorsal side, articles 2–6 subequal in size and shape, article 7 short, subconical, with four terminal sensory cones.

Collum large and broad, extending about 0.5 mm beyond ends of following tergite on each side, its surface smooth and polished, anterior

marginal ridge distinct. Anterior and posterior edges symmetrically tapering laterad to the rounded ends.

Paranota of segments 2–4 generally similar, paranota directed slightly cephalolaterad, anterior and posterior corners broadly rounded, lateral marginal swelling only slightly developed. Segments 5–15 similar, paranota more or less directly transverse, with peritremata larger and more strongly defined; anterior corners rounded, posterior corners subrectangular, becoming somewhat more acute on more caudal segments. Paranota depressed, moderately interrupting slope of dorsum, scapulorae entirely marginal, dorsal surface with distinct coriaceous sculpture, each paranotum with distinct low ovoid swelling within scapuloral arc.

Peritremata distinct, broad, flattened, elevated above adjoining surface of paranota; pores large and distinct, set near middle of peritreme, opening dorsolaterad. Metatergites medially smooth, becoming coriaceous towards paranotal bases; prozonites smooth, slightly elevated above level of metatergites at middorsal region, but the two subsegments meeting at a common level further laterad and ventral. Posterior edges of paranota not margined.

Tergites of segments 16–19 becoming narrower, with paranota increasingly produced into acute angles, those of segment 19 forming short bluntly rounded lobes about 0.9 mm in length; width of segment 19 between paranotal bases 2.3 mm.

Epiproct of usual subtriangular outline, dorsally convex and wrinkled transversely; ventrally concave; with usual two transverse whorls of setae and four apical setae. Paraprocts slightly convex, smooth except for few oblique grooves on outer basal quadrant, mesial margins smooth and strongly elevated, setiferous discal tubercule small and located close to midlength of mesial margin. Hypoproct broadly rounded, paramedian setiferous, tubercules small and inconspicuous, median terminal projection not strongly developed.

Sides of metazonites mostly smooth except for distinctive oblique grooves extending caudoventrad toward legs from anterior end of paranota. Caudal edge of metazonite set off by fine but distinct elevated marginal ridge, preceded by a groove. Vertical low ridge above posterior legs of each segment, sometimes provided with few vaguely defined tubercules. Stricture broad, distinct, and well-defined down sides, its surface finely granular in contrast to smooth glossy surface of prozonite; structure narrowing to mere suture across sternal region, but with prozonite definitely elevated and slightly overhanging suture line.

Sternal surface of metazonites distinctly but gradually elevated behind stricture, forming thin, overhanging transverse ridge between coxae of posterior pair of legs, usually medianly flattened or depressed;

subcoxal lobes are distinct, but not precisely acute or spiniform; a small field of 6 to 10 setae adjacent to base of each posterior coxa, and a short transverse row of 4 or 5 setae running in from base of each anterior coxa.

Legs fairly long and slender, distal end of femora visible beyond paranota when extended laterad and viewed from above; coxae subtrapezoidal, slightly compressed, 1.25 mm in length and height, with small spine at ventodistal end; prefemora rather short, also compressed, 1.5 mm in length and 1.1 mm in height, ventrodistal spine conical, acute, about 0.75 mm long, curved slightly caudad; femora elongated, cylindrical, increasing in diameter from a narrow base, 2.75 mm in length, 0.37 mm in basal diameter, distal diamter 0.62 mm; postfemur, tibia, and tarsus each 0.40 mm in diameter and 1.0, 1.0, and 1.12 mm in length, respectively. Pretarsus slender, somewhat sinuately curved, distinctly compressed, with a large median and two smaller paramedian dorsal carinae, length about 0.37 mm. Length relationship of podomeres: $3>2>1>6>5=4$.

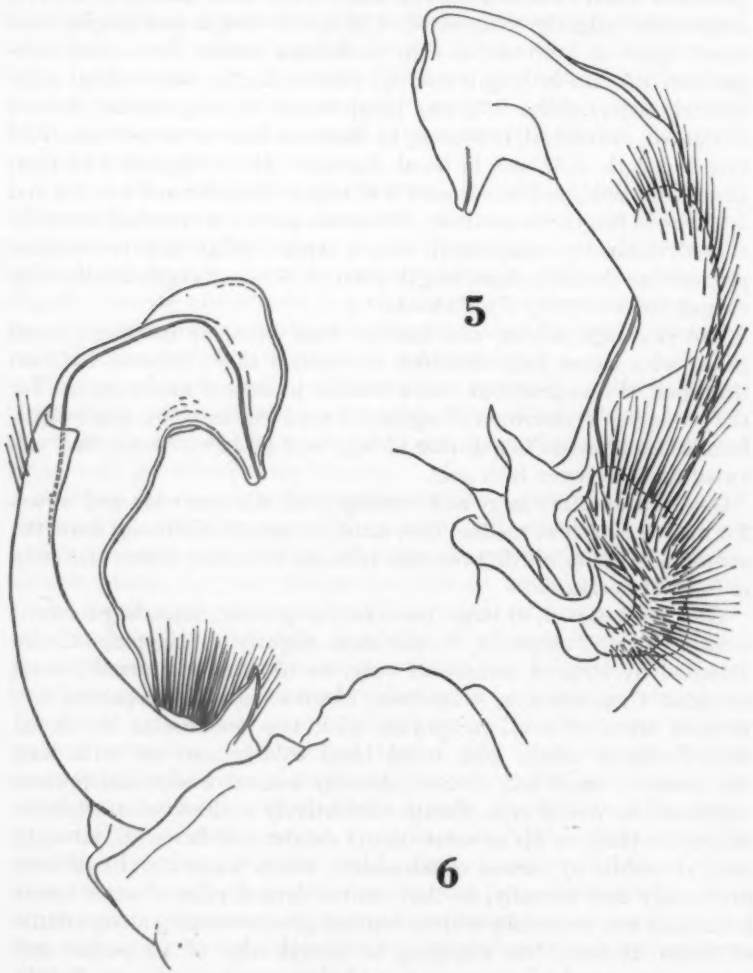
Anterior legs shorter and heavier than those at midbody, basal joints with dense long vestiture on ventral side. Sternum between third pair of legs produced into a median process of moderate size for the genus (fig. 3); sternum of segment 5 produced into two small digitiform lobes between fourth pair of legs, and into two broad, flat, elevated areas between fifth pair.

Gonopod aperture large and broadly oval, 4.5 mm wide and about 2.5 mm in length at median line, anterior margin distinctly indented across most of its width, prozonite reduced to narrow transverse strip in front of aperture.

Gonopods (figs. 5, 6) large, massive, compressed, extending forward between legs of segment 6, the ends slightly overlapping. Coxae attached by strip of membrane only, no distinct sclerotized sternal remnant. Coxa massive, subglobose, about as long as telopodital arc, without trace of coxal apophysis, with two macrosetae on dorsal side. Prefemur small, with usual basal enlargement set with long fine setae, a small but distinct, acutely conical prefemoral process originates on dorsal side. Femur (tentatively understood to include telopodite blade as far as setae occur) slender and flattened, strongly bent at middle by torsion of telopodite, which bends distal half both proximally and laterally, so that ventral lateral edge of outer femur is brought into a mesial position. Seminal groove running along middle of femur at base, but changing to lateral edge of telopodite and forming two nearly right-angle turns before running out onto slightly developed short solenomerite.

Color in life said to be blackish dorsally, with yellow paranotal spots.

VARIATION.—Second male, from Newberry County, S.C., is similar in all respects except that the dorsal surface is more distinctly coriaceous, the hypoproct is produced into a distinct median lobe, and the subcoxal spines are more definitely formed. The gonopods of this specimen are slightly more elongate than those of the type-specimen



FIGURES 5, 6.—*Cleptoria macra* Chamberlin, left gonopod of male holotype: 5, medial aspect; 6, dorsal aspect.

but do not differ in proportion or general appearance otherwise. This specimen in life had reddish paranotal spots as normal for the genus.

Newberry County is about 50 miles southeast of the type-locality of *C. macra*. It is possible that additional material will show that specimens from the two places differ consistently enough to receive subspecific recognition, but such action can certainly not be made or even predicted on the basis of only two specimens.

DISTRIBUTION.—*Cleptoria macra* so far is known from only two localities in central and western South Carolina; however, it almost certainly occurs also in adjacent parts of western North Carolina. Specimens have been examined as follows:

SOUTH CAROLINA: GREENVILLE COUNTY: Taylors, ♂ holotype, ♀ paratype, collected by R.V. Chamberlin, Aug. 5, 1910, RVC. NEWBERRY COUNTY: upland mixed woods, 5.5 miles north of Chappelle, 1♂, collected by Leslie Hubricht, May 21, 1960, RLH.

***Cleptoria rileyi* (Bollman)**

This species originally was described (Bollman, 1888) in a very few lines that indicate little more than family characters, but because of the reference to the end of the male gonopod ("subsimilar to a bird's head") (p. 345) it was possible for Dr. Chamberlin to correctly suspect that *C. rileyi* was congeneric with his own *C. macra* when that name was proposed in 1939. It could not be known with certainty, however, that specific differences existed, and Chamberlin was able to contrast the two only by recourse to supposed differences in size and coloration. H. F. Loomis, who subsequently examined the type of *C. rileyi*, considered the two names to be synonymous, as the gonopods are indeed similar when seen under low magnification in situ. Having had the opportunity to study the types of both names, I can confirm their distinctness, which I think will be revealed by inspection of the gonopod drawings.

Specimens from eastern Alabama are obviously conspecific with typical *C. rileyi* but differ in details of the gonopod structure and, in my opinion, probably represent a recognizable terminal geographic race. O. F. Cook, who had studied one of the Alabama millipeds, had in fact even designated it as a full species by the manuscript name *Fontaria alabama*.

Cleptoria rileyi as a species differs from other members of the genus chiefly in gonopod characters as set forth in the foregoing key. The telopodite lacks all traces of a prefemoral process, the apical part of the postfemur is broadly lobate on the outer margin with the extreme distal end directed proximad toward the coxa, the solenomerite is convex and striate, and the seminal groove is bent at an acute angle.

The two presumptive subspecies of *C. rileyi* are best separated by small details of the telopodite form, as seen in medial aspect (cf. figs. 7 and 9):

Postfemur with at most a very moderate marginal flange along the inner side; retrorse part of the apex relatively narrow and tapering (north-central and northeastern Georgia) . . . . . **rileyi rileyi** (Bollman)

Postfemur with a very prominent broad flange on the inner surface (fig. 9, pff); reflexed apical part of telopodite relatively much broader (east-central Alabama). **rileyi alabama,** new subspecies

Cleptoria rileyi rileyi (Bollman), new status

FIGURES 2, 7, 8, 12

Fontaria rileyi Bollman, 1889, p. 345.
Cleptoria rileyi.—Chamberlin, 1939, p. 9.—Chamberlin and Hoffman, 1958, p. 28.

TYPE-SPECIMEN.—Adult male holotype, USNM 2742, from Macon, Bibb County, Ga., collected by Lucien M. Underwood, August 1887.

DIAGNOSIS.—*Cleptoria rileyi* has been distinguished from its congeners under the species heading; the nominate subspecies contrasted with *C. r. alabama* by the characters cited in the above key couplet.

DESCRIPTION OF HOLOTYPE.—Length of body 40 mm (slightly contracted); width of sixth segment 11.0 mm, of twelth segment 10.5 mm; of sixteenth segment 10.0 mm. W/L ratio 27 percent (probably closer to 25 percent); W/D ratio at segment 12 62 percent.

Head smooth and polished, slightly convex, facial surface nearly flat; genae not margined, with distinct median impressions; labral setae about 18, clypeal setae about 14, series extended onto lower parts of genal margins. Vertigial, interantennal, and frontal setae not detected. Interantennal isthmus broad (1.5 mm) and flat, 20 percent of antennal length.

Antennae fairly long (7.5 mm) and slender, extending caudad to posterior edge of third tergite. Article 1 subglobose with few setae on dorsal side, articles 2–6 subequal in size and shape (1.4 mm in length), article 7 very short, subconical, with 4 terminal sensory cones.

Collum broad, extending about 0.5 mm beyond ends of following tergite on each side, its surface smooth and polished, anterolateral marginal ridge distinct. Anterior and posterior edges symmetrically tapering laterad to ends.

Body segments from second caudad with paranota transverse, none swept forward, anterior corners broadly rounded, posterior either rectangular or with peritremata slightly projecting beyond caudal margin. Paranota depressed, only slightly interrupting slope of middorsum, scapulorae strictly marginal, dorsal surface smooth or very minutely coriaceous, each paranotum with distinct ovoid swelling

within scapuloral arc. Peritremata distinct and elevated above adjoining surface of paranota even on second and third segments. Pores large and distinct, set near middle of peritreme, opening dorsolaterad. Metatergites medially smooth but becoming slightly coriaceous near base of paranota; prozonites smooth, slightly elevated above level of metatergites at middorsal region but the two subsegments meeting at a common level further laterad and ventrad. Posterior edges of paranota not margined.

Paranota of segments 16–18 distinctly acute triangular in shape, somewhat more coriaceous and with peritremata relatively more elevated than on preceeding segments. Paranota of segment 19 in the form of small oblong-ovoid lobes.

Epiproct of usual subtriangular outline, dorsally convex and transversely wrinkled, ventrally concave; with usual two transverse whorls of setae and four terminal setae. Paraprocts nearly flat, smooth except for few oblique grooves on outer basal quadrants, mesial margins very distinct and strongly elevated. Hypoproct broad, semicircular in outline, paramedian setal sockets not set on raised tubercules and slightly removed from margins, no median projection formed.

Pleural surfaces mostly smooth except for distinctive oblique grooves extending caudoventrad toward legs from anterior end of paranota. Caudal edge of metazonite set off by a fine but distinct elevated marginal ridge, this becoming more distinct dorsally. Vertical low ridge above second legpair of each segment, sometimes with a few vaguely defined tubercules. Stricture broad, distinct, and well defined down sides, its surface very finely granular in contrast to smooth glossy texture of prozonite; furrow narrows down to broad suture across sternal region but with prozonite definitely elevated and slightly overhanging suture line.

Sternal surfaces distinctly but gradually elevated caudad behind stricture, almost horizontal between legs or even shallowly depressed, glabrous except for small field of setae near base of each coxa. No trace of production into subcoxal spurs or angles.

Legs fairly long (7.5 mm) and slender, distal end of femora visible beyond paranota when extended and viewed from above; coxae posterior to gonopods with very small ventral spines, these increasing in size caudally; prefemora with short acute spines. Podomeres becoming increasingly setose from nearly glabrous femur, tarsus with numerous ordinary setae and terminal group of larger and longer setae around base of pretarsus. Latter of normal size and shape for family, somewhat bisinuate and distinctly compressed, with large median and two smaller paramedian dorsal carinae. Lengths of podomeres in decreasing order: 3–6–2–5–4–1.

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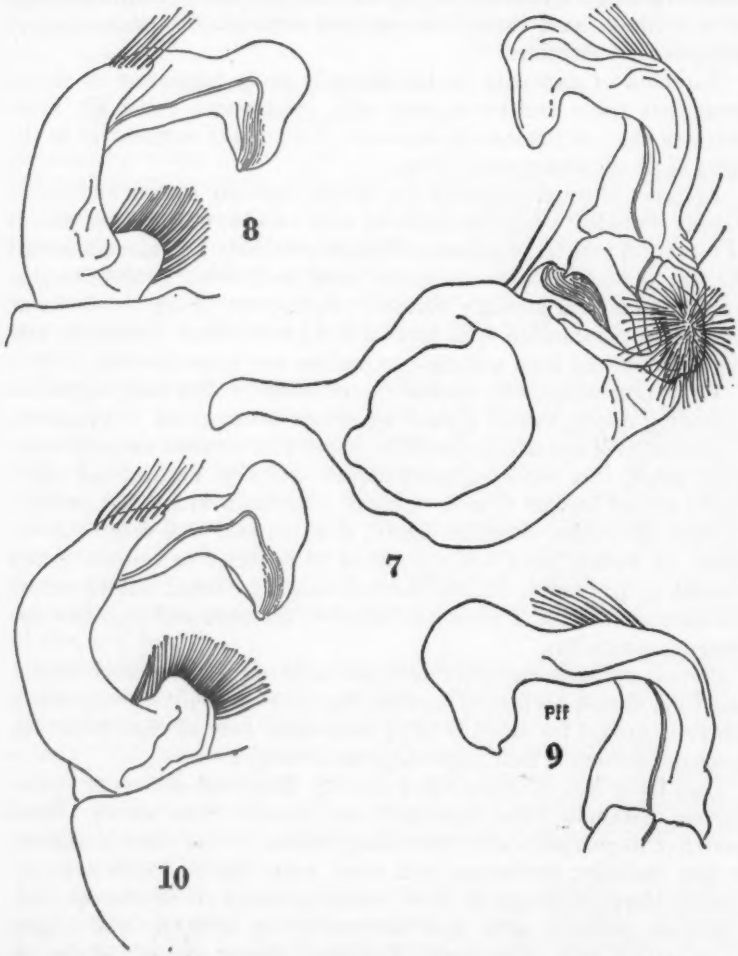
Anterior legs shorter and heavier than those at midbody, basal joints with dense long vestiture on ventral side. Sternum between third legpair produced into usual narrow apically bilobed process; sternum between fourth legpair with two small erect digitiform lobes; sternum between fifth legpair with two broad flat elevated areas.



FIGURES 7–10.—*Cleptoria rileyi* (Bollman), male gonopods: 7, *C. r. rileyi*, medial aspect; 8, *C. r. rileyi*, dorsal aspect; 9, *C. r. alabama*, new subspecies, left gonopod, medial aspect; 10, *C. r. alabama*, left gonopod, dorsal aspect.

Gonopod aperture broadly oval, its lateral ends broadly rounded and extending laterad beyond both coxal sockets and stigmata. Lateral edges with rounded margins, anterior and posterior edges about level with adjoining segmental surface. Prozonite reduced to narrow transverse strip in front of aperture.

Gonopods large and massive, telopodites exte ding cephalomesad with apical halves usually overlapping. Each coxa subglobose, distally slightly produced into short subcylindrical portion at coxotelopodital joint; length of coxae, exclusive of sternal apodeme, about equal to length of telopodite. No coxal apophyses formed, upper side with two or three subterminal macrosetae in usual position. Prefemur globosely enlarged, about equally bisected by seminal groove into convex glabrous elevation on coxal side, and densely setose region on adcoxal side. No indication of prefemoral process evident. Femoral division of telopodite broad, compressed, with distinct projecting marginal lobe on coxal side; femur rather strongly curved at about midlength, bringing distal half of gonopod mesially over base, dorsal margin produced into wide thin flange. Femoral division terminated by distinct obliquely transverse constriction that is subtended by field of large setae, texture of postfemoral surfaces much smoother and more shiny. Postfemur apically bent proximad at more than right angle, outer edge of arc produced into large rounded lobe adjacent to bisecting axis of angle formed by seminal groove (fig. 7); distal half of postfemur strongly convex, forming elevated, striate ridge carrying seminal groove out to bluntly acuminate tip of gonopod. Mesal side of postfemur with small but distinct submarginal flange.

According to Bollman, the type-specimen shortly after preservation was dorsally brownish with red paranota, the antennae, legs, and underparts yellow. The several specimens in my collection, however, appear to have had yellow paranotal spots and yellow legs prior to preservation. Obviously, additional field observations are desirable to confirm this apparent polymorphism in coloration.

DISTRIBUTION—Central to northeastern Georgia, in the Piedmont region. There is so far a lacuna of nearly 100 miles between Macon, Ga., and Auburn, Ala. (where the species is represented by a geographic variant); certainly specimens eventually will be discovered in west-central Georgia also. The following material has been examined:

GEORGIA: BIBB COUNTY: Macon, ♂ holotype, collected by L. M. Underwood, August 1887, USNM. CLARKE COUNTY: wooded hillside, 9 miles west of Athens, 1 ♂, collected by Hubricht, May 6, 1961. PUTNAM COUNTY: upland oak woods, 6 miles northeast of Eatonton, 1 ♂, collected by Hubricht, May 7, 1960, RLH. LINCOLN COUNTY: 4.2 miles south of Lincolnton, 1 ♀, collected by Hubricht, May 1, 1960, RLH [agrees structurally with males of *C. rileyi* and is in the right geographic area to be this species].

***Cleptoria rileyi alabama*, new subspecies**

FIGURES 9, 10, 12

HOLOTYPE.—Male, USNM 3245, also six male and female topoparatypes, from Auburn, Lee County, Ala., collected by O. F. Cook, July 1896.

DIAGNOSIS.—Similar to *C. r. rileyi* in most respects but differing in more strongly produced sternal areas and in details of gonopod structure, particularly appreciably larger flange of femoral portion as seen in mesal aspect (cf. figs. 9 and 10).

DESCRIPTION OF HOLOTYPE.—Length, ca. 44 mm, width of sixth segment 12 mm, of twelfth segment 12.8 mm, of sixteenth segment 11.0 mm; W/D ratio at twelfth segment 61 percent.

Agrees in details with description of *C. r. rileyi* but with following exceptions:

Collum not distinctly broader than following tergite.

Hypoproct with distinct median projection.

Podosterna more strongly modified, produced into subacute conical lobes between bases of posterior legs of each segment, but most distinctly developed on segments 8–14. Many of these segments also have sterna produced into low but distinct transverse ridge running mesally from base of coxa of each of anterior legs, these ridges carrying transverse row of setae noted for other subspecies. Interzonal furrow very pronounced down sides and deepest just in front of large, auriculate stigmata, edge of prozonite here emphasized as suberect, acute-edged flange.

Caudal edge of sides of segments set off by conspicuous elevated marginal ridge running from paranota down to upper end of coxal openings, becoming higher and more distinct ventrally, this ridge preceded by well-defined submarginal furrow similar to that of *Deltotaria brimleii*. Lower sides with short ridge just above coxae, variously denticulate and much more prominent than in two related subspecies.

Sterna between third legs produced strongly distad into medially suturate, apically somewhat divergent process, sternum between fourth legs with two processes as described for *C. rileyi* but these about twice as long, attaining level of ventral surface of adjacent coxae.

Gonopods generally similar to those of *C. r. rileyi* but somewhat more abruptly curved in femoral division and with adcoxal femoral flange larger and better defined; in mesal aspect tibiotarsal part of gonopod is distinctly more massive than corresponding area in *C. rileyi*.

DISTRIBUTION.—Known so far only from east-central Alabama. The following material, all topotypical, has been examined:

ALABAMA: LEE COUNTY: Auburn, ♂♂♀♀, types, collected by O. F. Cook, July 1896, USNM; 4.5 miles southwest of Auburn, 1 ♂, paratype, collected by L. Hubricht, Apr. 4, 1960, RLH.

***Cleptoria bipraesidens*, new species**

FIGURE 11

HOLOTYPE.—Adult male, USMN 3246, from Jefferson, Jackson County, Ga., collected by Leslie Hubricht, Apr. 4, 1953.

DIAGNOSIS.—A species of Rileyi Group characterized by distal end of gonopod, which is slender and elongate and without striations parallel to seminal groove, and by color pattern of transverse red crossbands.

DESCRIPTION OF HOLOTYPE.—Length ca. 45.0 mm, width of sixth segment 11.0 mm, width of twelfth segment 11.0 mm, width of sixteenth segment 10.0 mm. L/W ratio 24 percent; W/D ratio at segment 12 59 percent.

Structural details in general as described for *C. rileyi* but with following exceptions:

Antennae slightly longer in proportion, 8.0 mm in length; interantennal isthmus wider, 1.7 mm, 21 percent of antennal length.

Collum not broader than following tergite.

Peritremata less distinctly elevated, somewhat broader and flatter than in *C. rileyi*, their lateral edges slightly sinuous on poriferous segments. Dorsal surface of paranota less coriaceous, nearly as smooth as middorsal area.

Paraprocts smooth but mesial margins elevated abruptly only along ventral half. Above level of marginal setae, margins only slightly elevated and merging gradually into discal paraproctal surface. Hypoproct broadly triangular in outline with distinct median projection.

Sterna produced into low but distinct subconical lobes at bases of posterior pair of legs, these lobes most distinctive on segments 8–14. Row of 3–6 large setae extending mesad from coxal base of each leg of anterior pair; sternal lobes between posterior legs of each segment carrying rounded field of about 12–18 setae, this arrangement constant for most segments.

Posterior edge of gonopod aperture distinctly elevated into high flange above intercoxal surface of segment 7. Gonopods similar to *C. rileyi* except that recurved distal part of telopodite is flat instead of strongly convex, distinctly more slender and elongated, and seminal grooved not paralleled by numerous striations.

Color in life black dorsally, with posterior corners of paranota, broad transverse band on caudal edges of metatergites, and circumference of collum red; underparts grayish white, legs pink basally, becoming reddish distally.

REMARKS.—This species so far is known only from the holotype, with the result that details of cyphopod structure, seasonal occurrence, and geographic range must await future discoveries for elaboration. There can be no doubt that *C. bipraesidens* is closely related to *C. rileyi*, but sufficient differences between the two insure specific separation.

FIGURE 11.—*Cleptoria bipraesidens*, new species, left gonopod of male holotype, dorsal aspect.

***Cleptoria abbotti*, new species**

FIGURES 4, 12–16

TYPE-SPECIMENS.—Male holotype and female paratype, USNM 3103 (D–729), three male and three female paratypes (RLH), from 5 miles southwest of Waynesboro, Burke County, Ga., collected by Leslie Hubricht, May 22, 1960.

DIAGNOSIS.—Large member of genus with exceptionally short and massive gonopods, subapical rounded lobe of telopodite partly reflexed laterodorsad, apical lobe strongly convex and striated; sternal process between third pair of legs extending well beyond lower surface of adjoining coxae.

DESCRIPTION OF HOLOTYPE.—Adult male, length of body 49.5 mm (somewhat contracted), width of sixth segment 12.2 mm, of twelfth segment 12.8 mm, of sixteenth segment 11.3 mm. W/L ratio 26 percent; W/D ratio at segment 12 57 percent.

Structurally quite similar to *C. rileyi* with following exceptions: genae evenly convex without median impressions; antennae relatively shorter 8.4 mm, 65 percent of maximum body width as opposed to 71 percent in *C. rileyi;* interantennal isthmus relatively broader in proportion to antennal length, 24 vs. 20 percent in *C. rileyi.*

Dorsal surface of paranota essentially flat, lacking the median discal convexity of *C. rileyi* and other species. Ozopores opening dorsally on peritremata instead of somewhat dorsolaterally.

Hyproproct with small but distinct median projection between setiferous tubercules.

FIGURE 12.—Distribution of four species of *Cleptoria* in Georgia and adjoining areas of Alabama and South Carolina.

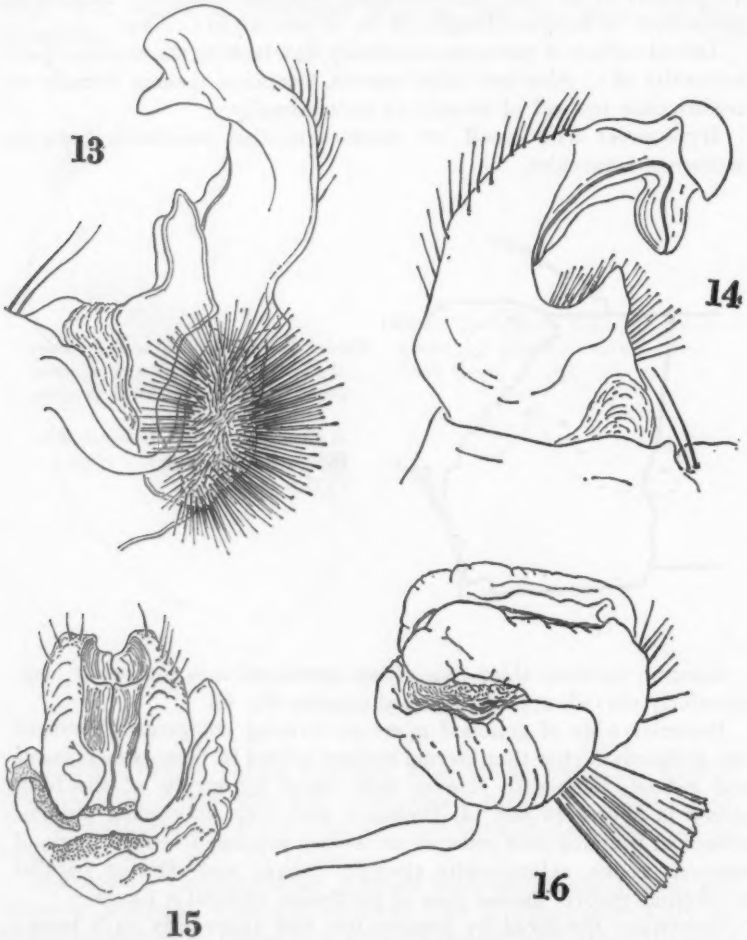
Sternum between third pair of legs produced into unusually long, anteriorly curved, apically notched process (fig. 4).

Posterior edge of gonopod aperture forming compressed elevated rim distinctly higher than sternal surface behind it. Gonopods massive and robust, telopodite shorter than usual for genus, of the form shown in figures 13 and 14. Prefemur with erect subconical process; subapical rounded lobe reflexed somewhat proximad toward angle of seminal groove, solenomerite strongly convex and striated parallel to seminal groove; medial face of postfemur without a flange.

Specimens discolored by preservation but apparently dark brown dorsally in life, with paranotal spots and distal podomeres dark reddish pink.

PARATYPE.—Adult female, length about 46.3 mm, width of segment 6 11.9 mm, of segment 12 12.8 mm, of segment 16 11.5 mm; W/L ratio about 28 percent. Structurally similar to male except for usual sexual differences: shorter and more slender antennae, relatively broader sterna, and more slender legs.

Cyphopods rather massive, receptacle largest on median or posterior side, strongly ridged vertically, curving around in front of valves and slightly around to anterior or lateral side of latter (fig. 15). Valves



FIGURES 13–16.—*Cleptoria abbotti*, new species: 13, left gonopod of holotype, medial aspect; 14, same, dorsal aspect; 15, left cyphopod of female paratype, caudoventral aspect; 16, same, medial aspect.

essentially similar in size and appearance, largest basally, attenuated toward free ends, distally concave to enclose flat impressed surface traversed by median suture. Operculum small, concealed in dorsal and medial aspects, under convex basal ends of valves.

REMARKS.—In addition to the eight specimens from the type-locality, *Cleptoria abbotti* is known from a single male taken 2.8 miles north of Cadley, Warren County, Ga. (collected by L. Hubricht, May 30, 1960). Both of the localities are in the drainage system of Briar Creek, a tributary of the Savannah River. This area was for many years the residence of the early American amateur arachnologist John Abbott, and it seems entirely appropriate to associate Abbott's name with a species of milliped apparently endemic to the region in which he carried on his work.

***Cleptoria divergens* (Chamberlin), new combination**

This moderate sized, somewhat disjunct species was described originally in *Sigmoria*, and, in fact, the male gonopod corresponds well to the diagnosis given for that genus: "Includes large, robust species which are characterized by the sigmoidally curved blade of the telopodite." By actual comparison, however, with typical sigmorias such as *S. munda*, *S. aberrans*, *S. mariona*, and *S. conclusa*, the gonopod of *S. divergens* assumes a quite different appearance. The termination of the telopodite, when seen from the correct perspective, is broadened considerably and provided with a large rounded subapical lobe quite reminiscent of that so characteristic of *C. rileyi* and *C. abbotti*. It seems preferable to me to reassign *S. divergens* to the genus *Cleptoria* although it is almost as "divergent" there as in *Sigmoria* and the species is unquestionably a credit to its name.

There is striking geographic variation in the color pattern of this relatively localized form. Chamberlin's types were black with red dorsal markings and legs; in going southwest along the Blue Ridge, the red pigment changes to an intense dark bluish purple that merges with the black ground color. As there is a small but distinctive geographic range occupied by these two variants, I think they may be distinguished by subspecific names as shown in the following key:

Metatergites nearly black with caudal margins and paranotal spots red; basal podomeres yellow, distal four reddish . . . **divergens divergens** (Chamberlin)
Metatergites nearly black, with caudal margins and paranotal spots deep violet purple; legs whitish, reticulated with black . . **divergens nigrescens** (Hoffman)

***Cleptoria divergens divergens* (Chamberlin), new status**

FIGURES 1, 17–19, 21

Sigmoria divergens Chamberlin, 1939, p. 8, figs. 19–21.—Hoffman, 1950, p. 28.—Chamberlin and Hoffman, 1958, p. 49.

TYPE-SPECIMENS.—Male holotype and numerous topoparatypes, RVC, from Landrum, Spartanburg County, S.C., collected by R. V. Chamberlin, Aug. 4, 1910.

DIAGNOSIS.—With characters of the species, distinguished from *C. d. nigrescens* by presence of normal red pigmentation of metatergites and legs.

DESCRIPTION (male from Greenville Co., S.C.).—Length 43.7 mm, width of segment 6 10.0 mm, of segment 12 9.9 mm, of segment 16 9.8 mm. W/L ratio 23 percent; W/D ratio at midbody 65 percent.

Structural features essentially as in *C. rileyi* with following exceptions: interantennal isthmus slightly broader, 24 percent of antenna length instead of 20 percent; antennae about 7.5 mm long.

Paranota essentially transverse from segments 2 through 14; their dorsal surface nearly flat. Peritremata weakly set off from adjoining surface, continuous with caudal edge of paranota on segments 2 through 4. Paranota of segment 19 in form of subtriangular lobes.

Caudal sides of metazonites smooth and unmodified, lacking distinct marginal ridge, preceded by groove. No low ridge above posterior pair of legs of segments.

Sterna of metazonites with fairly distinct subcoxal acute lobes between legs of posterior pair. Coxae of legs posterior to gonopods with very prominent ventral spines; prefemora with moderately long acute distal spines.

Posterior edge of gonopod aperture forming distinctly elevated flange. Gonopods large, directed cephalad, telopodites interlocked in situ. Coxa without peculiarities, usual two macrosetae on dorsal side. Prefemur somewhat more elongated than in other species, with small acutely laminate process on dorsal side. Gonopod beyond prefemur forming sigmoidally curved acropodite without subdivisions evident; curvature first ventromedial, thence abruptly expanded with prominent lobation on the outer side, seminal groove running out onto small short "solenomerite" as seen in dorsolateral aspect (fig. 19), this terminal area corresponding closely in shape to telopodite ending in other species of genus with shorter and more massive gonopods.

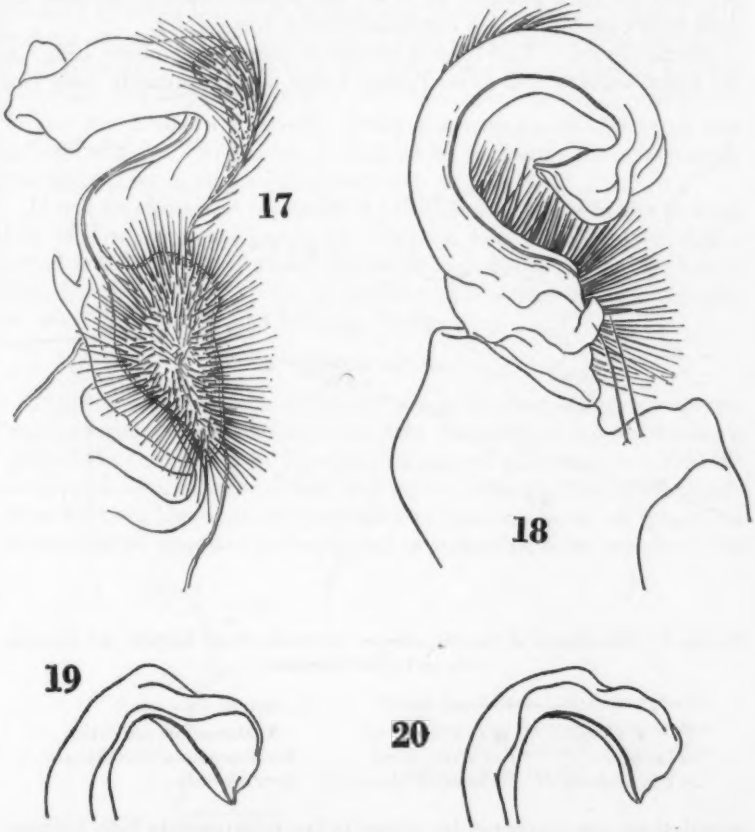
Sternal processes of third segment somewhat shorter than in other species of *Cleptoria* (fig. 1).

Dorsum blackish, with caudolateral halves of paranota and transverse marginal band on each metatergite reddish; sides of segments whitish with vertical red stripe; basal podomeres yellowish, distal four segments pink.

DISTRIBUTION.—Foothills and eastern escarpment of Blue Ridge along western edge of Greenville County, S.C. Almost certainly it will be found in the adjoining North Carolina counties of Henderson and Rutherford; probably the valley of the French Broad River forms the northwestern boundary of the range (see fig. 21).

Specimens from the vicinity of Caesar's Head, S.C., appear to be intermediate both in gonopod form and color pattern with the nominal subspecies *C. n. nigrescens;* the locality is indicated on the map by an X. Specimens have been examined from the following localities:

SOUTH CAROLINA: Spartanburg County: Landrum, ♂♂♀♀, types, collected by R. V. Chamberlin, Aug. 4, 1910, RVC. Greenville County: 1.5 miles east of North Carolina state line on U.S. Hy. 25, 1♂, 2♀, collected by L. Hubricht, June 24, 1950, RLH. Pickens County: 1 mile west of Caesar's Head on U.S. Hy. 276, 4♂, collected by Hubricht, June 24, 1950, RLH [intergrades with *C. d. nigrescens*].



Figures 17–20.—*Cleptoria divergens* (Chamberlin): 17, *C. d. divergens*, left gonopod, medial aspect; 18, same, dorsal aspect; 19, same, apex of telopodite, caudolateral aspect; 20, *C. d. nigrescens* (Hoffman), caudolateral aspect of apex of telopodite.

***Cleptoria divergens nigrescens* (Hoffman), new combination, new status**

Figure 20

Sigmoria nigrescens Hoffman, 1950, p. 28, figs. 28–32.—Chamberlin and Hoffman, 1958, p. 51.

Type-specimens.—Male holotype and female paratype, USNM 1880 (D–193); male paratype, RLH, from Sassafras Mountain on

U.S. Hy. 178, 1 mile north of intersection with S.C. Rt. 228, ca. 4 miles south of Rocky Bottom, Pickens County, S.C.; collected by R. L. Hoffman, July 15, 1949.

DIAGNOSIS.—Similar to nominate subspecies in structural details except for slight difference in termination of gonopod (cf. figs. 19 and 20), and for color pattern, in which red pigmentation is replaced by dark bluish purple, almost concolorous with dorsal color.

DISTRIBUTION.—This form is known to occur on the Blue Ridge in the strict sense as well as on Pisgah Ridge, and presumably these two

FIGURE 21.—Distribution of *Cleptoria divergens* in western South Carolina and adjoining counties in North Carolina.

———state line ----------county lines

○ *C. d. divergens* ● *C. d. nigrescens* X intermediate population
1=Landrum 3=Caesar's Head 5=Horsepasture River Gorge
2=U.S. Highway 25 4=Sassafras Mountain 6=Pink Beds

populations are connected by others in the intermediate high country west of Brevard, N.C., around the headwaters of the French Broad River (see fig. 21). The following specimens have been examined:

SOUTH CAROLINA: PICKENS COUNTY: south slope of Sassafras Mountain, 1 mile west of intersection with S.C. Hy. 288, on U.S. Hy. 178, 2 ♂♂, 1 ♀, types collected by R. L. Hoffman, July 15, 1949, USNM, RLH.

NORTH CAROLINA: TRANSYLVANIA COUNTY: Field station of Highlands Biological Station in Horsepasture River Gorge, ca. 4 miles south of Lake Toxaway, 4 ♂, 4 ♀, collected by W. H. Adams and J. R. Paul, July 16, 1961; Chubb Gap Trail, Pink Beds Recreation Area, ca. 8 miles north-northwest of Brevard, 1 ♀, collected by R. L. and Marian S. Hoffman, July 30, 1958; 2 ♂, 1 ♀, July 13, 1962.

REMARKS.—The type-specimens from South Carolina were uniformly blackish dorsally; the material from the Pink Beds area according to field notes, were nearly black with the paranota a delicate pinkish violet.

From what little is known so far, *C.d. nigrescens* at least shows a strong partiality for moist woods with rhododendron thickets. Individuals are apparently nocturnal, as many man-hours of collecting at Pink Beds have turned up only four specimens, in contrast to literally hundreds of *Cherokia georgiana!* One hour spent in the Horsepasture Gorge was fruitless although during the evening of the same day Adams and Paul picked up a small series and saw others in exactly the same place in which I had collected.

It will be of interest to establish additional localities in the western half of Transylvania County as this form almost certainly makes a swing around the headwaters of the French Broad River. Probably, also, future work will reveal it further to the southwest in the gorges of the Whitewater and Chatooga Rivers.

Relationships

There is no doubt that *Cleptoria* is related most closely to several genera, notably *Sigmoria* and *Brachoria*, occurring in the southeastern part of the United States. Beyond this general statement, it is difficult to present detailed comparisons for several reasons. First, the distinctions between these genera (or species groups) are based on subjective evaluation of gonopod patterns and are thus liable to personal bias

FIGURE 22—Schematic diagram of possible phylogeny in *Cleptoria*, the most primitive species on the right, the more specialized toward the left.

in interpretation. Secondly, *Sigmoria* as presently known appears to be somewhat heterogeneous and perhaps divisible into two or more groups. Finally, quite a number of species, some of them possibly annectant in their characters, remain to be discovered and published.

With the exception of *C. divergens*, however, the species here referred to *Cleptoria* share such a distinctive basic gonopod configuration

that identification of a male specimen as a *Cleptoria* can be made with the unaided eye. As implied by its name, *C. divergens* has a somewhat less characteristic gonopod and rather approximates a structure one might consider as fairly typical of *Sigmoria*. Perhaps this species represents a level of evolution just beyond that of the dichotomy separating the stocks ancestral to present members of these two genera. Certain species of *Cleptoria* appear to be closely related in the gonopod structure as indicated by the very provisional

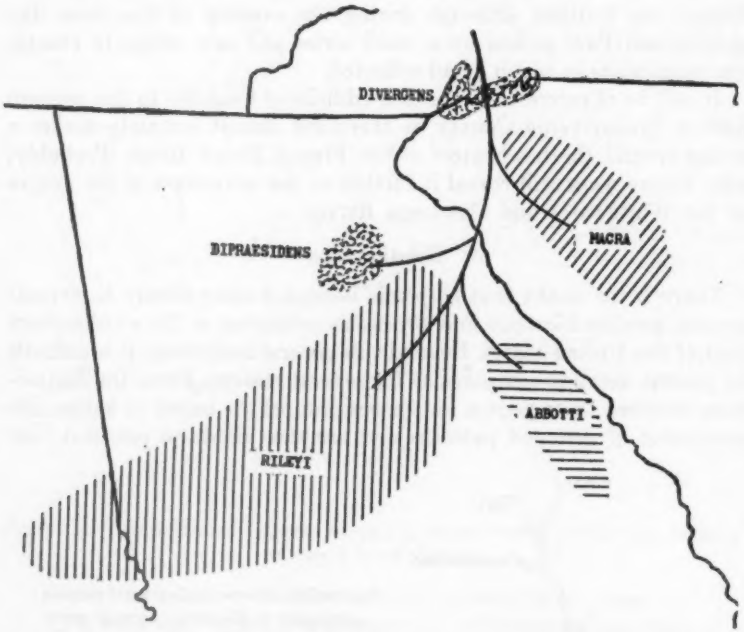


FIGURE 23.—Superposition of phylogenetic dendrogram from figure 22 upon the known distribution of species of *Cleptoria*.

diagram in figure 22. The overall appearance of the appendage is judged in guessing at affinities and not single "key-characters" that, although obvious, probably have little significance in phylogenesis. The presence or absence of a prefemoral process, for instance, constitutes such a character.

By the assumption that the gonopod of *C. divergens* represents a relatively unspecialized form, it is possible to arrange the species of *Cleptoria* in a tentative evolutionary sequence with *C. abbotti* representing the extreme development: its gonopod is especially shortened

and robust, with a massive and convex solenomerite, and the sternal processes of the third segment are the most prominent in the genus. Obvious affinity is seen with *C. rileyi*, which has a somewhat more slender telopodite, and with *C. bipraesidens*, in which the solenomerite is longer and not notably thickened. These three species might be considered as making up a single group. *Cleptoria macra* is intermediate between the members of this group and *C. divergens*. On the diagram (fig. 22), the presumed sequence of specialization runs from right to left.

A second diagram (fig. 23) shows the remarkably good "fit" that obtains when the foregoing derivation is superimposed on the present distribution of the various species. Although species of *Sigmoria* now occur widely in the South Carolina Piedmont and may be sympatric with *C. macra* at the present, the majority of species of that genus occur in the Southern Appalachians. It seems reasonable to suspect that the ancestral lineage of *Cleptoria* developed in that area and subsequently migrated south and west through the Piedmont of Georgia. There is some indication that speciation may have occurred in a sort of straight-line (perhaps "leap-frog") sequence rather than by in situ speciation from a single widespread ancestral form.

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